

Acoustic Communication in Crickets (Orthoptera: Grylloidea): A Model of Regressive Evolution Revisited Using Phylogeny

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ABSTRACT

Acoustic communication is essential in cricket biology, being related to mating behavior. Current hypotheses on the evolution of acoustic communication in crickets consider that singing is ancestral in crickets, and that it has been lost several times in different cricket lineages. According to studies of cricket populations, it has also been hypothesized that the loss of acoustic communication could have occurred following a progressive transformation series. Similarly, it has been assumed that several factors could have influenced that evolution, such as predation pressure, low efficiency of acoustic communication due to poor environmental conditions, an evolutionary shift toward another mode of communication, population structure or habitat of the taxa. I present a phylogenetic test of this model. Song characteristics were optimized onto the phylogenetic trees for two clades of cricket (Grylloidea, Phalangopsidae) and the resultant phylogenetic patterns compared with the theoretical patterns implied by the pre-existing hypotheses. My study produced four main results: (1) multiple and convergent absences of songs occurred; (2) no linear and progressive transformation series toward complete song loss was found; (3) the polarization of the presence/absence of songs was not always in the sequence predicted by the model; (4) reversals from song lack to song presence were documented. Such reversals have never been hypothesized before, and the acoustic evolution of crickets appeared highly homoplastic. Phylogenetic analyses showed that factors such as predation pressure, population structure, etc., cannot be characterized on the basis of their definite evolutionary effect on acoustic communication: consequently previous hypotheses on their possible influence on cricket evolution cannot be tested. Although many papers have been written on acoustic communication in crickets, no clear and general hypothesis yet exists for its origin and evolution. Integrated studies of both phylogeny and population biology are badly needed to generalize the results presented in this paper, and to support new hypotheses on the subject.

RÉSUMÉ

La communication acoustique chez les Grillons : un modèle d'évolution régressive testé à l'aide de la phylogénie

La communication acoustique occupe une place importante dans la biologie des grillons, principalement dans le contexte de la reproduction. Les hypothèses classiques sur l'évolution acoustique des grillons considèrent que ce mode de communication leur est ancestral, et qu'il a été perdu au cours de l'évolution à de multiples reprises et de manière indépendante. À partir d'études de populations, un modèle d'évolution a ainsi été proposé, selon lequel la communication acoustique aurait été perdue à plusieurs reprises de manière progressive, suivant des étapes bien définies. Pareillement, des hypothèses ont été émises sur les facteurs susceptibles d'influencer l'évolution acoustique chez les grillons (prédation, efficacité de ce mode de communication dans le milieu ambiant, habitat, structure des populations, évolution vers un autre mode de communication).

DESUTTER-GRANDCOLAS, L., 1997. — Acoustic communication in crickets (Orthoptera: Grylloidea): A model of regressive evolution revisited using phylogeny. In: GRANDCOLAS, P. (ed.), *The Origin of Biodiversity in Insects: Phylogenetic Tests of Evolutionary Scenarios. Mém. Mus. natn. Hist. nat.*, **173** : 183-202. Paris ISBN : 2-85653-508-9.

Un test phylogénétique de ces hypothèses est présenté, à partir des analyses phylogénétiques de deux clades de grillons (Grylloidea, Phalangopsidae). Les patterns phylogénétiques obtenus par optimisation des chants sur la phylogénie de ces deux clades sont comparés aux patterns théoriques dérivés des hypothèses testées. L'hypothèse de convergences pour l'absence de chants est confirmée par l'analyse phylogénétique ; la progressivité des pertes n'est cependant pas corroborée, et la polarisation des absences ou présences des chants n'est pas forcément celle prédite par le modèle. Des réversions sont par contre documentées, ce qui n'avait jamais été envisagé auparavant. L'évolution acoustique apparaît finalement fortement homoplasique chez les grillons. Les analyses phylogénétiques montrent également que les facteurs tels que prédation, structure de populations, ..., ne peuvent pas être caractérisés les uns par rapport aux autres par leur effet supposé sur la communication acoustique : les hypothèses évolutives proposées à leur sujet ne sont pas exclusives, et ne peuvent dans leur forme actuelle se prêter à une procédure de test. Bien que la communication acoustique des grillons ait fait l'objet de nombreuses études, aucune hypothèse claire n'existe actuellement sur son origine et ses modalités d'évolution. Des études conjointes en phylogénie et en biologie des populations seront ainsi nécessaires d'une part pour généraliser les résultats déjà obtenus sur les Phalangopsidae, et d'autre part pour proposer de nouvelles hypothèses sur la question.

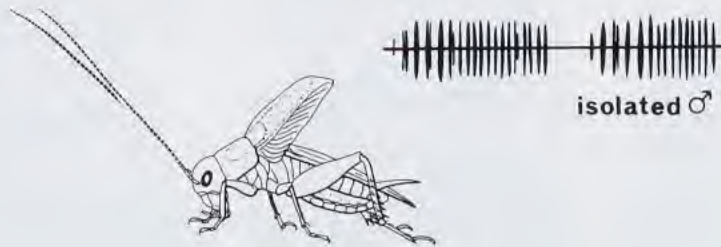
INTRODUCTION

Acoustic communication plays a leading role in cricket biology. In most species it is associated with mating. Songs are emitted by males only (Fig. 1), either to attract distant females (calling songs), to attract and keep the females at close range (courting songs) or to chase male intruders (aggressive songs) (CHOPARD, 1938; HUBER *et al.*, 1989). Singing is achieved by means of a special forewing apparatus called the stridulum (Figs 2-8). This apparatus is complex, both regarding its structure and its operative mode (MICHELSEN & NOCKE, 1974; SISMONDO, 1979; KOCH *et al.*, 1988; BENNET-CLARK, 1989; DESUTTER-GRANDCOLAS, 1995a), and it is widely and exclusively distributed in crickets. It is thus currently considered ancestral in this clade (ALEXANDER, 1962, 1967; OTTE, 1977, 1992; WALKER & MASAKI, 1989).

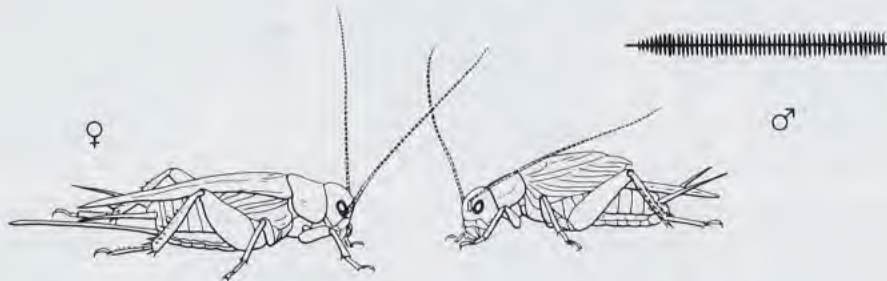
The question of how acoustic behavior has evolved in crickets has long been debated. ALEXANDER (1962, 1967, 1987) postulated that originally cricket songs were similar to courting songs, emitted at close range. The subsequent evolution of acoustic communication in crickets would have been achieved by the diversification of the emitted signals, which would have been driven by two factors: the growing number of potentially interacting acoustically signaling species (each species being characterized by at least its calling song), and an increase in the number of functions for the signals. ALEXANDER (*op. cit.*) thus assumed that the calling song derived from the courting song, and the aggressive song from the calling song (see also BAILEY, 1991): "The only soft, close-proximity signals among modern crickets are courtship sounds, and it is likely that this reproductive context was the one in which the first cricket chirp was produced. All the other signals are probably outgrowths of this fundamental situation" (ALEXANDER, 1987: 84).

The acknowledgment that not all crickets are able to sing (Figs 3, 6, 8) has led other authors to consider that singing may have been lost many times in crickets. This evolution toward muteness has been hypothesized to follow several steps based upon the life habits of extant species (OTTE, 1977, 1990, 1992; WALKER & MASAKI, 1989; BAILEY, 1991). These steps, outlined in figure 9, include: 1) Ancestrally, species sang and had three song types. 2) In some circumstances, the calling song may have become facultative, singing and non-singing (satellite) males living in close proximity. 3) The calling song was definitively lost, but courting and aggressive songs still existed. 4) Species became mute, even though they still retained the stridulum. 5) The stridulum was finally lost. This loss may or may not have been followed by the loss of auditory organs (OTTE, 1990).

CALLING SONG



COURTING SONG



AGGRESSIVE SONG



FIG. 1. — The three main songs emitted during mating by crickets (modified from LOHER & DAMBACH, 1989). Sonagrams of the songs in frames.

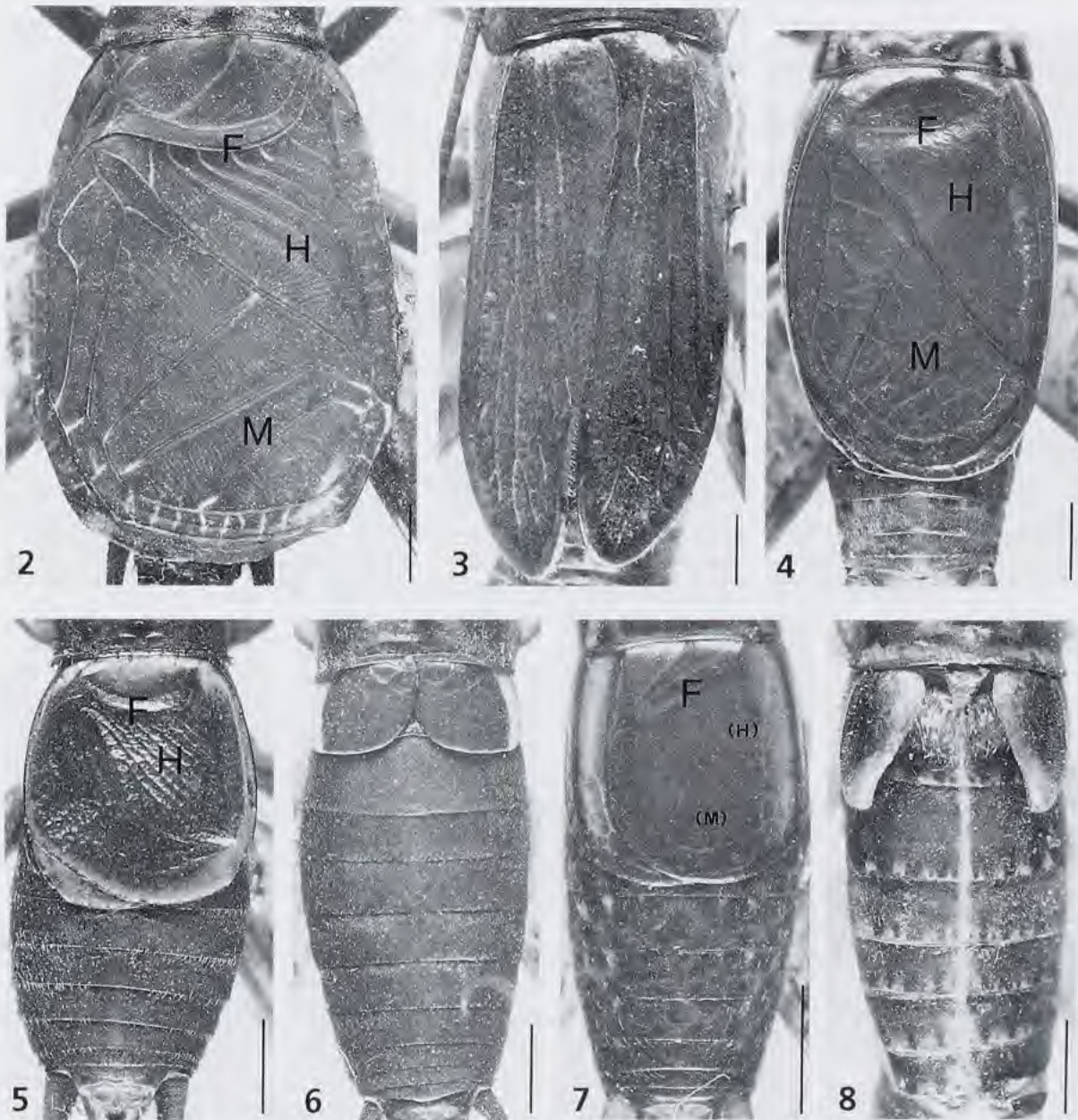
Current hypotheses on the acoustic evolution in crickets thus assume that 1) songs have evolved progressively from the courtship song, 2) the ancestral stridulum and songs have been lost several times in different cricket lineages, and 3) both the loss of the stridulum and that of the songs have been achieved according to a definite and linear transformation series. No reversal of this gradual song loss has ever been hypothesized. In order to analyze the evolution of

acoustic communication in crickets, it is necessary to consider separately the evolution of the stridulum and that of the acoustic repertoire. Although these traits are obviously connected (in crickets, song *s.str.* is only emitted by the stridulum), there exists no obligatory correspondence between definite states of the stridulum and the extent of acoustic repertoires (OTTE, 1977, 1992).

Hypotheses of stridulum loss have been tested in a phylogenetic context (DESUTTER-GRANDCOLAS, 1997). Phylogenetic patterns support the hypothesis of a convergent loss of the stridulum. They did not support, however, the progressive disappearance of the stridulum: a functional stridulum could be lost in only one evolutionary step, without intermediary conditions. A high level of homoplasy was also documented for diverse stridulum types, and phylogenetic patterns indicate that reversal could occur. Finally the stridulum appeared evolutionarily labile.

I will consider here the hypotheses about the evolution of the cricket songs. I will not however analyze whether courting is the ancestral song type in crickets, as this would have to be tested at a higher phylogenetic level. Supposing that the ancestral acoustic repertoire of true crickets comprises a calling, a courting and an aggressive songs, current assumptions on their acoustic evolution could be described by a definite sequence of song combinations (Fig. 9). This sequence implies that the loss of the songs is ordered, the calling song disappearing first, followed by the courting and the aggressive songs. Given this only three of the eight possible combinations of the three songs should exist (Fig. 10). Again no reversal is hypothesized. Here I will perform phylogenetic tests of these theoretical patterns and ask if song loss is the only possible evolutionary change in the acoustic evolution of crickets.

Dealing with the patterns of acoustic evolution in crickets, one cannot help asking which factors may have influenced it. Four factors have been hypothesized to have played a role in the evolutionary reduction of cricket acoustic repertoire (HUBER *et al.*, 1989; OTTE, 1992). Is it possible first to characterize the potential influence of each factor, and second to test it using phylogeny? The first, and most strongly advocated factor is predation. Both parasites and predators are supposed to be attracted by calling individuals, thereby influencing long range signals (CADE, 1975; BURK, 1982; THORNHILL & ALCOCK, 1983; BAILEY, 1991). For crickets, this means that the calling song could be affected, but not the courting or the aggressive songs, which are emitted at short range. The second factor is the environment, in particular the environment's effect on the efficiency of acoustic signal transmission (RÖMER, 1993). Communication occurs between a sender(s) and a receiver(s). Efficient communication allows the receiver(s) to know who calls, what for and from where. Physical problems in sound propagation in the natural environment may alter the information conveyed by acoustic signals, especially for pure-tone signals such as cricket calls (MICHELSEN & NOCKE, 1974; RÖMER & LEWALD, 1992 *in* RÖMER, 1993). Acoustic signals emitted simultaneously can also mask each other (RÖMER, 1993). Finally some environments have been supposed unfavorable for acoustic communication because of their physical properties or because of their noisiness (for example caves or shores, respectively; OTTE, 1992). Environmental constraints are thus more likely to interfere with long range signals (RÖMER, *op. cit.*) than with short range signaling. Population structure and habitat have been hypothesized to influence song loss via sedentariness (WALKER, 1974) or confinement (BOAKE, 1984a, b), respectively (see also ALEXANDER, 1962). The idea is that individuals that stay together can find each other by chance without any special attractant



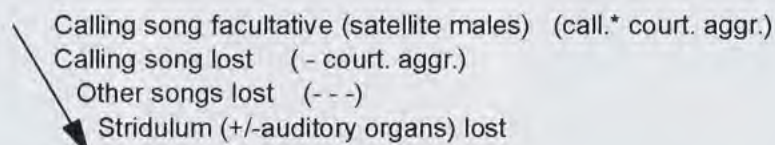
FIGS 2-8. — Diversity of tegminal structures in phalangopsid crickets. 2: *Noctivox sanchezi* (Amphiacustae), with a normally developed, non corneous stridulum. 3: *Phaeophilacris* sp., with tegmina modified for communication through air puffs (DAMBACH & LICHTENSTEIN, 1978). 4: *Luzarida guyana* (*Luzarida* group), with a normally developed stridulum, but a corneous right tegmen. 5: *Paragryllodes* sp., with a reduced, though functional stridulum. 6: *Cantrallia huasteca* (Amphiacustae), with non overlapping tegmina and no functional stridulum. 7: *Luzaridella clara* (*Luzarida* group), with an incomplete stridulum and a corneous right tegmen. 8: *Eidmanacris multispinosa*, with deeply modified tegmina probably showing glandular structures (DESUTTER-GRANDCOLAS, 1994b). Stridulum: F, file; H, harp, M, mirror. Scales: 2 mm.

CURRENT MODEL FOR ACOUSTIC EVOLUTION IN CRICKETS

1/ Ancestral condition: 3 song types (*calling, courting, aggressive song*)

2/ Multiple, independent losses

3/ Several definite steps toward muteness



4/ No reversal hypothesized

FIG. 9. — Current model on the evolution of acoustic communication in crickets (references in the text).

SONG COMBINATIONS PREDICTED BY THE TESTED MODEL

1/	Call.	Court.	Aggr.
2/	-	Court.	Aggr.
3/	-	-	-

SONG COMBINATIONS NOT PREDICTED BY THE TESTED MODEL

4/	Call.	Court.	-
5/	Call.	-	Aggr.
6/	Call.	-	-
7/	-	Court.	-
8/	-	-	Aggr.

FIG. 10. — List of song combinations that could exist in crickets. Names of songs: Call.: calling song; Court.: courting song; Aggr.: aggressive song (references in the text).

signal. Here again the long-range signal would be lost. The fourth factor that has been hypothesized to influence song evolution is the evolutionary shift toward another communication mode. Chemical (OTTE, 1977, 1992) and visual (TOMS, 1986; BAILEY, 1991) shifts have been proposed as replacement communication systems. Vibrational communication has also been recorded in crickets (LOHER & DAMBACH, 1989), however there is currently no suggestion that it replaced acoustics. Chemical and visual signals are efficient at both long and short range, visual

FACTORS CURRENTLY HYPOTHESIZED TO BE RESPONSIBLE FOR ACOUSTIC
EVOLUTION OF CRICKETS, AND THE SONG REPERTOIRE THEY IMPLY

- 1/ Predation: (Call. Court. Aggr.) » (- Court. Aggr.)
 - 2/ Inefficiency of acoustic communication: (Call. Court. Aggr.) » (- Court. Aggr.)
 - 3/ Population structure / Habitat : (Call. Court. Aggr.) » (- Court. Aggr.)
 - 4/ Shift toward another communication mode
 - A/ At long range only : (Call. Court. Aggr.) » (- Court. Aggr.)
 - B/ At long range, and at short range between M/F and M/M: (Call. Court. Aggr.) » (- - -)
 - C/ At long range, and at short range between M/M: (Call. Court. Aggr.) » (- Court. -)
 - D/ At long range, and at short range between M/F: (Call. Court. Aggr.) » (- - Aggr.)
 - E/ At short range between M/F: (Call. Court. Aggr.) » (Call. - Aggr.)
 - F/ At short range between M/M: (Call. Court. Aggr.) » (Call. Court. -)
 - G/ At short range between M/F and M/M: (Call. Court. Aggr.) » (Call. - -)
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FIG. 11. — Current hypotheses on the factors that could have influenced the acoustic evolution of crickets (references in the text).

cues being efficient only in daylight. At long range, these signals would replace the calling song. At short range, they could play a role in interactions between male and female and replace the courting song, or between males only and replace the aggressive song, or in both kinds of interactions, replacing both the courting and aggressive songs. Operating over both long and short ranges, these signals could potentially replace all types of songs.

Figure 11 shows the different song combinations that would result from the influence of each factor on the evolution of acoustic communication in crickets. It is clear that these factors are not mutually exclusive, and that a given sequence of songs is predicted by more than one factor. For example, the loss of the calling song is expected from the influence of predation, inefficiency of acoustic communication, population structure, habitat type or a shift toward another long range communication mode. This overlap precludes a test of the influence of these factors. Some song combinations, however, appear specific of one factor.

I present here a phylogenetic test of current hypotheses on the modalities of the acoustic evolution in crickets, and on the factors that could have influenced it. For this I will confront the theoretical patterns these hypotheses imply with the results of my phylogenetic analyses on two monophyletic cricket clades, the *Amphiacustae* and the *Luzarida* group (Grylloidea, Phalangopsidae). In each clade the optimization of song types onto the phylogeny allows me to derive evolutionary scenarios on the acoustic evolution of the clade. These scenarios may or may not fit the theoretical patterns and may or may not corroborate the hypotheses under study (CODDINGTON, 1990; CARPENTER, 1989; BROOKS & MCLENNAN, 1991; MCLENNAN, 1991; GRANDCOLAS *et al.*, 1994). For practical reasons, the hypotheses on the factors will be analyzed using the *Amphiacustae* clade only.

MATERIAL AND METHODS

Two monophyletic groups of phalangopsid crickets (Grylloidea, Phalangopsidae) were used in this study: the Amphiacustae (DESUTTER-GRANDCOLAS, 1993a, 1994a) and the *Luzarida* group (DESUTTER-GRANDCOLAS, 1993b). Their phylogeny has been previously analyzed with cladistics, using Wagner parsimony and the option implicit enumeration of the Hennig86 program (FARRIS, 1988). Data matrices were built with unweighted morphological and anatomical characters; multi-state characters were coded as non additive. No song characters were then included in the matrices because of the lack of evident primary homologies (DE PINNA, 1991; GRANDCOLAS *et al.*, 1994).

For the present paper, song data were collected from the literature and from my own personal observations in the field. They were treated as attributes (MICKEVICH & WELLER, 1989) and optimized on the cladograms using Wagner parsimony. Each song was treated as one attribute, with two possible states (present/absent). Three attributes were considered: calling song (Call.), courting song (Court.) and aggressive song (Aggr.).

The Amphiacustae (Figs 12, 14) comprise nine genera distributed in Central America and the West Indies. Cladistic analyses of morpho-anatomical characters resulted in one phylogenetic tree (CI = 0.92, RI = 0.95, 28 steps) (DESUTTER-GRANDCOLAS, 1993a, 1994a). Two monophyletic species groups exist in the genus *Mayagrillus*: one group (*Mayagrillus* 1) presents no tegmina, that is no acoustic apparatus; the other (*Mayagrillus* 2) includes two apterous species (no stridulum) and one species with reduced, not corneous tegmina and a functional stridulum. Songs have been described by ALEXANDER & OTTE (1967) for *Amphiacusta* and BOAKE (1983, 1984a, b) for *Nemoricantor*. I have observed *Noctivox* and *Cantrallia* in their natural habitat. *Arachnopsita*, *Leptopedetes* and *Mayagrillus p.p.* have tegminal conditions that do not allow them to sing (DESUTTER-GRANDCOLAS, 1993a, 1996). No data exist on *Longuripes*, *Prolonguripes* and *Mayagrillus p.p.*

The *Luzarida* group (Figs 13-15) comprises nine genera distributed in the northern half of South America, east of the Andes. Cladistic analyses of morpho-anatomical characters resulted in one, incompletely resolved tree (CI = 0.80, RI = 0.86; 20 steps) (DESUTTER-GRANDCOLAS, 1993b). All available data on the singing behavior of the *Luzarida* group taxa (except *Palpigera*, the song of which is unknown) result from my own personal observations in the field.

RESULTS

The Amphiacustae

Song evolution. The states of the attributes are at least partly documented in 7 of the 9 genera of the Amphiacustae, and a complete series of attributes states is available for 5 of them (plus *Mayagrillus p.p.*). Acoustic communication has been completely described for 2 taxa (*Amphiacusta*, *Nemoricantor*); it is absent in 3 others (*Cantrallia*, *Leptopedetes*, *Arachnopsita*), plus *Mayagrillus p.p.* Mapping song attributes onto the cladogram (Fig. 14) shows that the three song types are not obligatorily present in any singing taxa (although they could be in *Noctivox*). *Amphiacusta* has no aggressive song, while it has a calling and a courting song. *Nemoricantor* on the contrary has only a courting and an aggressive song, but no calling song. The combinations of attributes states found in the Amphiacustae are (Call. Court. -), (Call. Court. Aggr.), (Call. Court. ?) and (- - -). All these combinations are predicted by the model depicted in Figure 9, except for (Call. Court. -). Also their distribution on the phylogeny of the Amphiacustae does not support the hypothesis of a linear transformation toward the loss of acoustic communication.

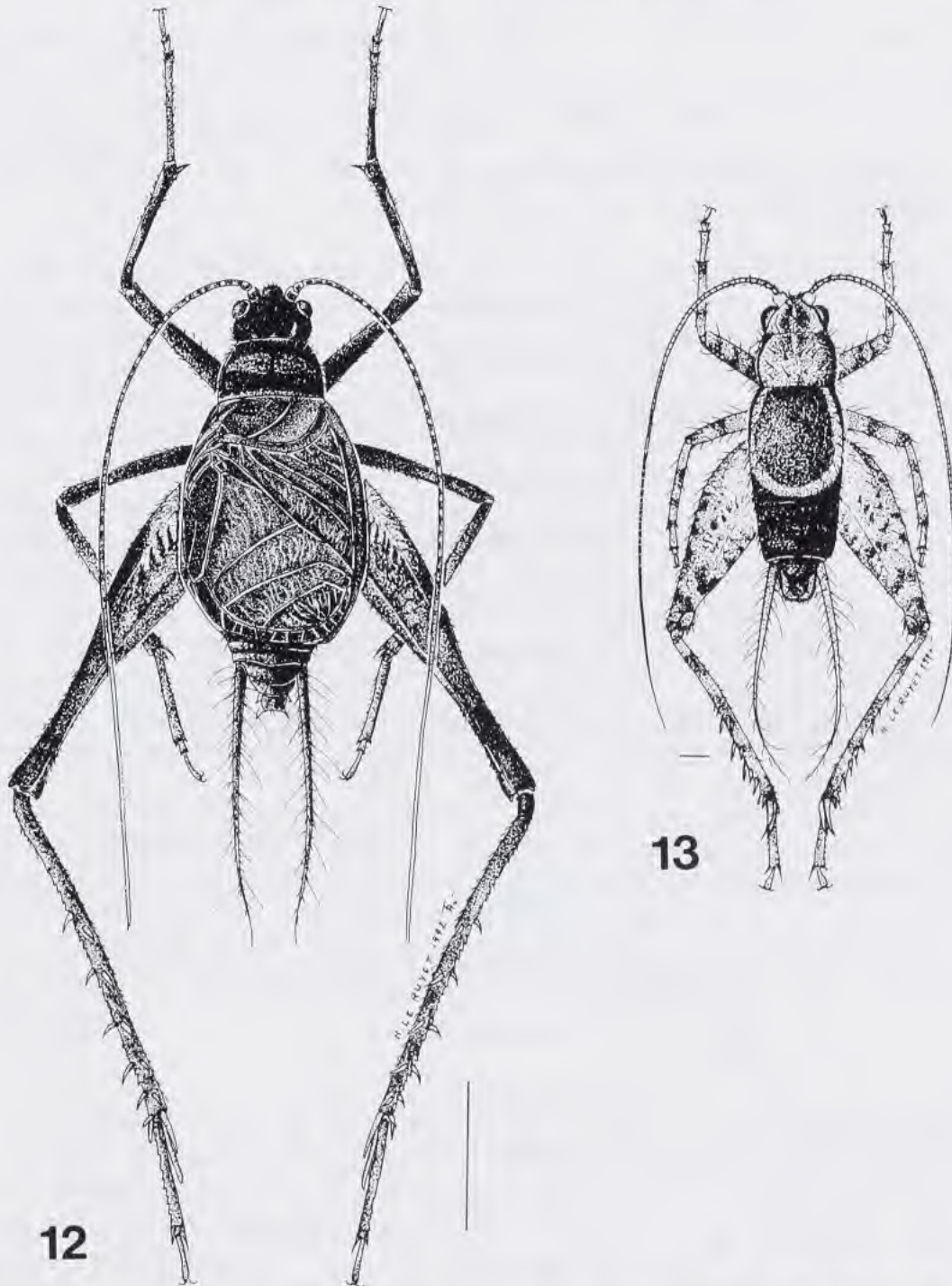
The scenarios derived for each attribute are as follows:

Calling song (Fig. 16). Three equally parsimonious scenarios exist, with two steps each.

- A) Calling song is ancestral; it is lost twice independently in *Cantrallia* and in the clade [*Leptopedetes* - *Mayagrillus*].
- B) Absence of calling song is ancestral; a calling song appears once in [*Amphiacusta* (*Noctivox* - *Cantrallia*)], and one subsequent reversal to ancestral condition occurs in *Cantrallia*.
- C) Absence of calling song is ancestral; two independent appearances of a calling song occur in *Amphiacusta* and *Noctivox*.

Courting song (Fig. 17). Four equally parsimonious scenarios exist, with 3 steps each.

- A) Courting song is ancestral; three independent losses of courting song occur in *Cantrallia*, *Leptopedetes* and in the subgroup [*Arachnopsita* - *Mayagrillus*].



FIGS 12-13. — 12: *Noctivox sanchezi* Desutter-Grandcolas, 1993a (Amphiacustae), scale: 5 mm. Note the well-developed stridulum. 13: *Ochraperites ottei* Desutter-Grandcolas, 1993b (*Luzarida* group), scale: 1 mm. Males in dorsal view, modified from DESUTTER-GRANDCOLAS, 1993a, 1993b. Note the consistency of tegmina and the type of stridulum (right tegmen with a stridulatory file only).

B) Courting song is ancestral; the courting song is lost twice independently in *Cantrallia* and in the clade [*Leptopedetes* - *Mayagrillus*], and one subsequent reversal occurs in *Nemoricantor*.

C) Absence of courting song is ancestral; a courting song appears twice independently in

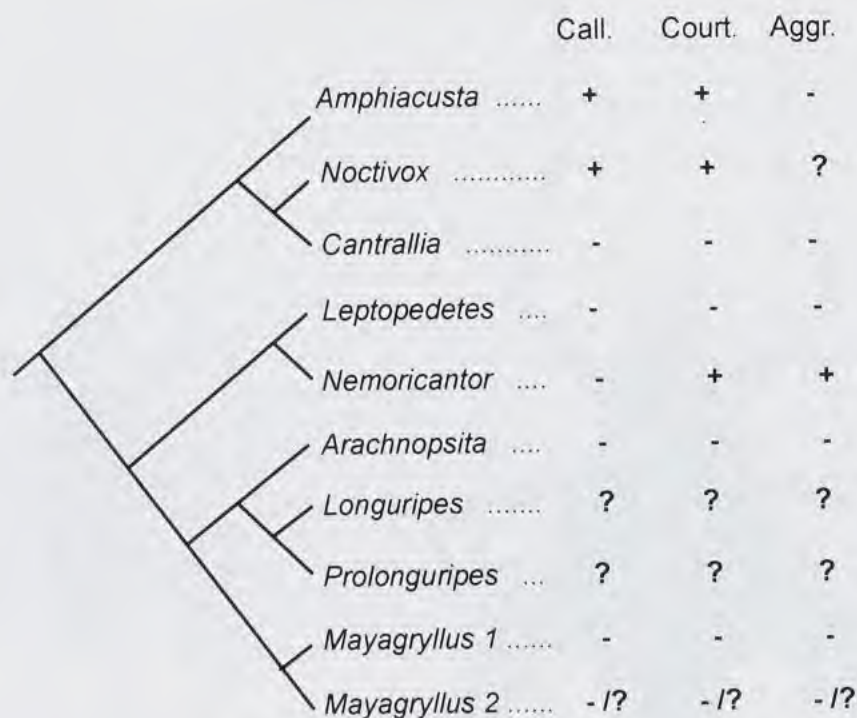


FIG. 14. — Phylogeny and song attributes in the Amphiacustae (Grylloidea, Phalangopsidae). Symbols for attributes: +: presence, -: absence; ?: state unknown.

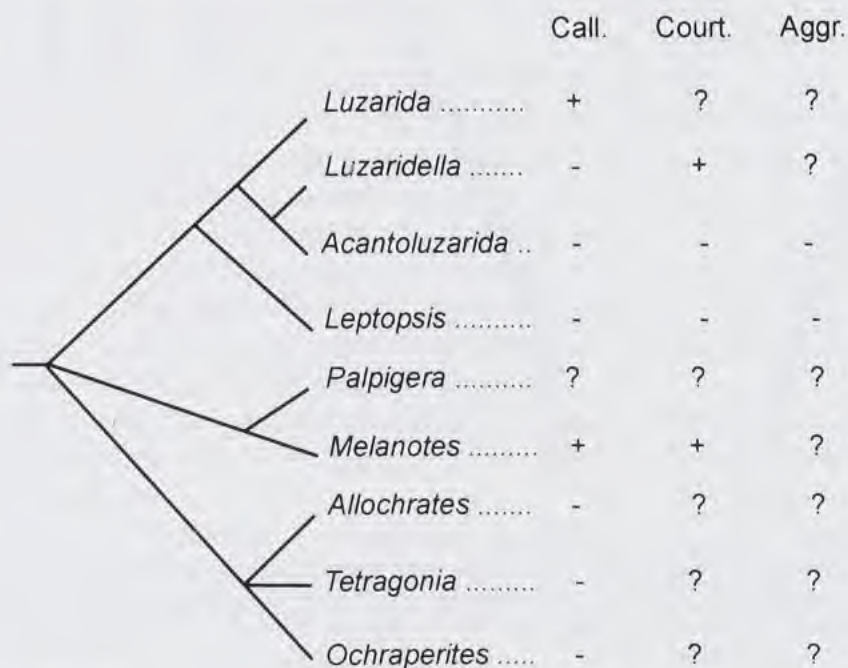


FIG. 15. — Phylogeny and song attributes in the *Luzarida* group (Grylloidea, Phalangopsidae). Symbols for attributes: +: presence, -: absence; ?: state unknown.

Nemoricantor and in the clade [*Amphiacusta* (*Noctivox* - *Cantrallia*)], and one subsequent reversal to ancestral state occurs in *Cantrallia*.

D) Absence of courting song is ancestral; three independent appearances of a courting song occur in *Amphiacusta*, *Noctivox* and *Nemoricantor*.

Aggressive song (Fig. 18). Only one most parsimonious scenario has been found (1 step). It implies an ancestral absence of the aggressive song and its subsequent appearance in *Nemoricantor*.

A combined analysis of all three attributes shows that 12 equally parsimonious scenarios (6 steps) could explain the present distribution of song types in the Amphiacustae (Fig. 19). The ancestral repertoire is ambiguous: it may comprise a courting or a calling song, both songs or neither; the aggressive song is ancestrally absent in all 12 cases.

All the scenarios show convergent modifications of the calling song, the courting song or both: the songs appear or disappear, according to the ancestral condition, in two or more taxa. For example, when the calling song is ancestrally absent, the scenarios always imply subsequent appearances of the calling song (Figs 19C - F, I - L); a similar situation occurs for the courting song (Figs 19G - L). Conversely, when the calling song (or the courting song) is ancestral in Amphiacustae, several convergent losses occur.

Factors of song evolution. Comparison with the theoretical song combinations (Figs 10-11) shows that only three of them exist in the Amphiacustae: (- Court. Aggr.) in *Nemoricantor*, (- - -) in *Cantrallia*, *Leptopedetes*, *Arachnopsita* and *Mayagryllus p.p.*, and (Call. Court. -) in *Amphiacusta*. These could support a potential effect of the following factors: predation, inefficient acoustic communication, population structure, habitat, evolution toward a pheromonal communication between males and females both at long and close range, and evolution toward a pheromonal communication between males at close range. One should remark however that these factors have always been supposed to have interfered with an ancestral song combination comprising all three song (Call. Court. Aggr.). Such an ancestral song combination is however not attested for the Amphiacustae, as the Amphiacustae ancestrally lack an aggressive song. This means that none of the evolutionary sequence hypothesized to test the influence of currently invoked factors is found in this group, and that no current hypothesis can account for present data on this clade.

The Luzarida group

Song attributes are not as well known in the *Luzarida* group as in the Amphiacustae, especially for the courting and the aggressive songs (Fig. 15): these attributes are known in four and two taxa respectively, two of them being deprived of a stridulum. A complete description of the attributes is thus available only for those non acoustic taxa (combination - - -). Other incomplete combinations are (Call. Court. ?), (- Court. ?), (Call. ? ?) and (- ? ?). These combinations are not incompatible with the tested model of the evolution of acoustic communication in crickets. According to available data, scenarios could be derived only for the calling and the courting songs.

Calling song (Fig. 20). Only one most parsimonious scenario (2 steps) exists. It implies an ancestral absence of the calling song, and two subsequent, independent appearances in *Luzarida* and in *Melanotes*.

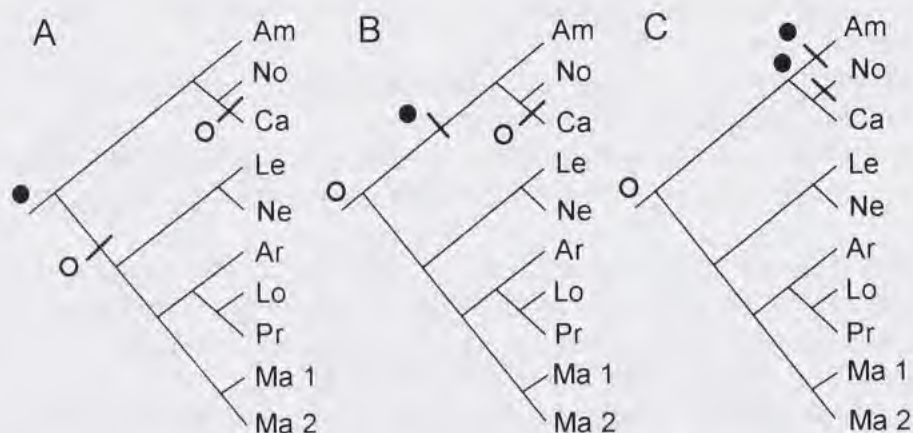


FIG. 16. — Equally parsimonious scenarios for the evolution of the calling song in the Amphiacustae. Symbols: black circle: presence; empty circle: absence; thick line: evolutionary change. Names of taxa: Am: *Amphiacusta*, Ar: *Arachnopsita*, Ca: *Cantrallia*, Le: *Leptopedetes*, Lo: *Longuripes*, Ma 1, 2: *Mayagryllus* (1, 2), Ne: *Nemoricantor*, No: *Noctivox*, Pr: *Prolonguripes*.

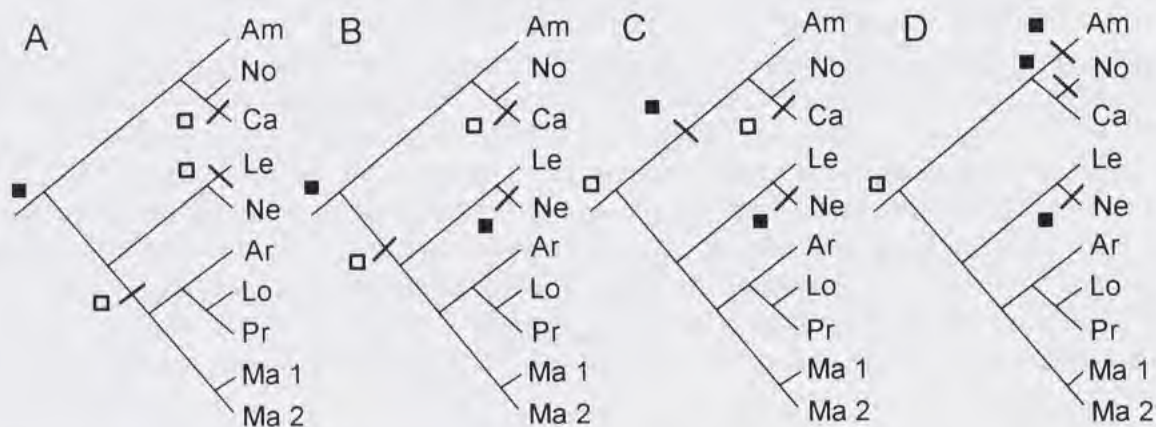


FIG. 17. — Equally parsimonious scenarios for the evolution of the courting song in the Amphiacustae. Symbols: black square: presence; empty square: absence; thick line: evolutionary change. Names of taxa as in figure 12.

Courting song (Fig. 21). Three equally parsimonious scenarios (2 steps) are possible.

A) Courting song is ancestral; it disappears twice independently in *Leptopsis* and in *Acantoluzarida*.

B) Courting song is ancestral; it is lost in the clade [*Luzarida* - *Leptopsis*]. A subsequent reversal occurs in *Luzarida*.

C) Absence of courting song is ancestral; a courting song appears twice independently in *Luzaridella* and in *Melanotes*.

The combined analysis of the calling and courting songs (Fig. 22) shows that 3 equally parsimonious scenarios exist for the acoustic evolution of the *Luzarida* group. They all have 4

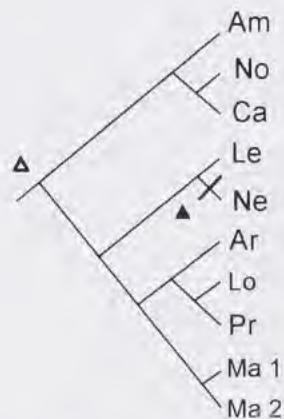


FIG. 18. — Parsimonious scenario for the evolution of the aggressive song in the Amphiacustae. Symbols: black triangle: presence; empty triangle: absence; thick line: evolutionary change. Names of taxa as in figure 16.

steps and imply convergent changes of the calling song and, for two of them, of the courting song too. The ancestral condition is absence of calling song, and presence or absence of courting song. It should be noted that in all these scenarios the ancestrally absent calling song reappeared twice independently, which does not corroborate the tested model.

DISCUSSION

What is the pattern of the evolution of acoustic communication in crickets?

Even if acoustic behavior is still incompletely known in the Amphiacustae and in the *Luzarida* group, the phylogenetic analyses of the available songs partly invalidate current proposals on the acoustic evolution of crickets. As already indicated above, the only hypothesis which cannot be tested with these data is whether the courting song is the ancestral song for crickets (ALEXANDER, 1967; BAILEY, 1991). However a courting song exists in all the taxa which emit acoustic signals, while calling and aggressive songs may be absent.

I will consider the following questions in turn: are song losses documented? Are the observed song combinations similar to those predicted by the model? Is the hypothesis of a linear (regressive) transformation of acoustic repertoire attested by the phylogenetic patterns?

Songs are lacking in several taxa in the studied clades. This lack may concern the whole three songs (mute taxa) or only one of them. The missing song is then either the calling song (*Nemoricantor* in the Amphiacustae, *Luzaridella* in the *Luzarida* group) or the aggressive song (*Amphiacusta* in the Amphiacustae). Both the absence of the calling song and the taxa muteness could support the model of a regressive evolution of cricket acoustic repertoire (Fig. 9). The absence of the aggressive song is however not consistent with it. Also the polarization of song absence according to phylogenetic patterns suggests that a song absence in a taxon does not necessarily mean that the song has been lost in that taxon. Song lack may be ancestral to a whole clade. This means that song lack can be apomorphic or plesiomorphic, and this also is not consistent with the model.

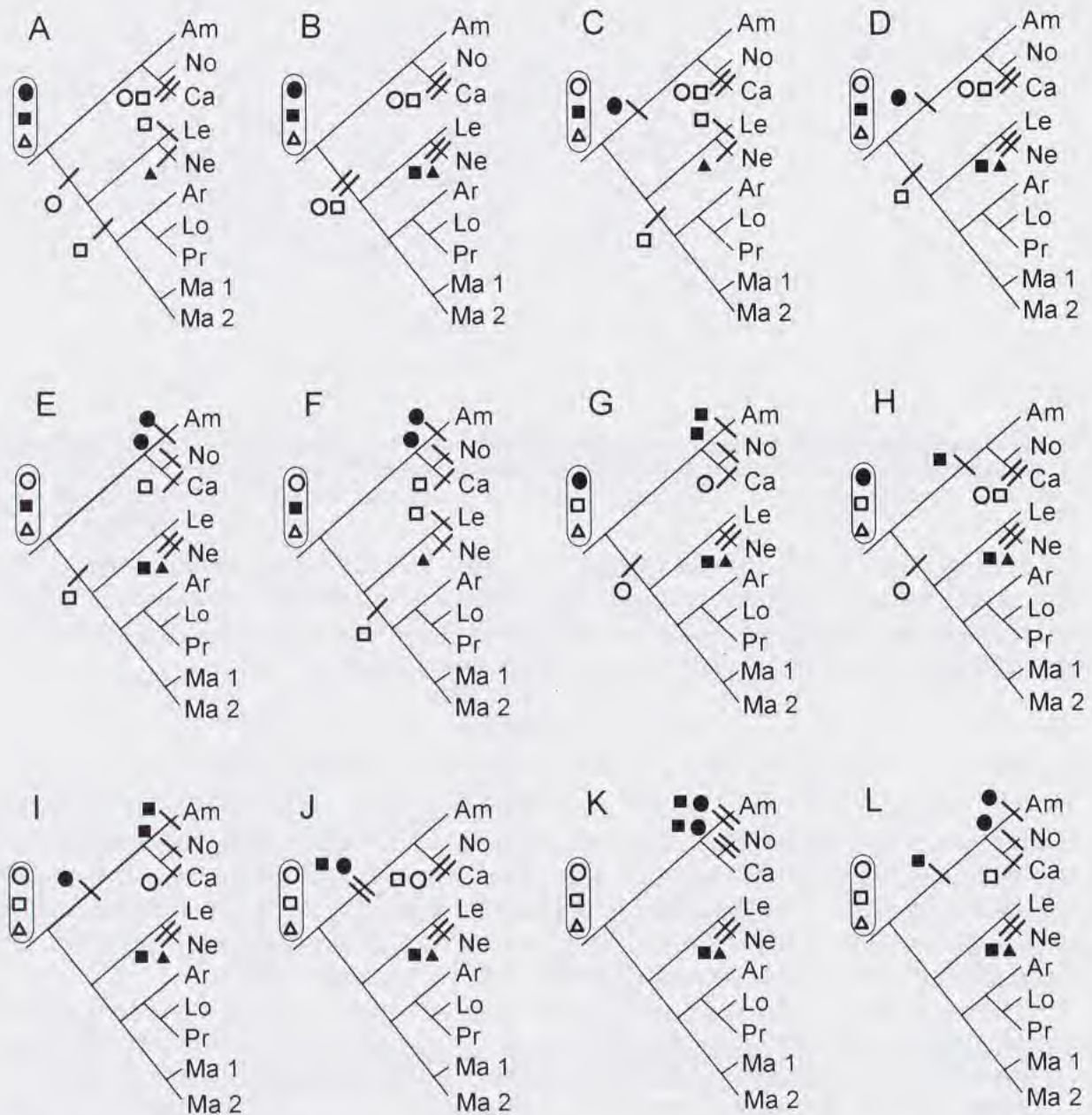


FIG. 19. — Equally parsimonious scenarios for the evolution of singing ability in the Amphiacustae. Symbols as in figures 16-18; ancestral states of attributes indicated in a frame. Names of taxa as in figure 16.

The song combinations assumed by the model shown in Figure 10 include (Call. Court. Aggr.) as the ancestral condition, with (- Court. Aggr.) and (- - -) as derived conditions. The last two combinations have been documented here. As mentioned above, however, the combination (Call. Court. Aggr.) does not represent the ancestral condition in the studied groups: the Amphiacustae ancestrally lack an aggressive song, while the *Luzarida* group is

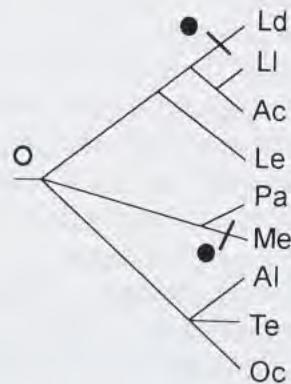


FIG. 20. — Parsimonious scenario for the evolution of the calling song in the *Luzarida* group. Symbols: black circle: presence; empty circle: absence; thick line: evolutionary change. Names of the taxa: Ac: *Acantoluzarida*, Al: *Allochrates*, Le: *Leptopsis*, Ld: *Luzarida*, Ll: *Luzaridella*, Me: *Melanotes*, Oc: *Ochraperites*, Pa: *Palpigera*, Te: *Tetragonia*.

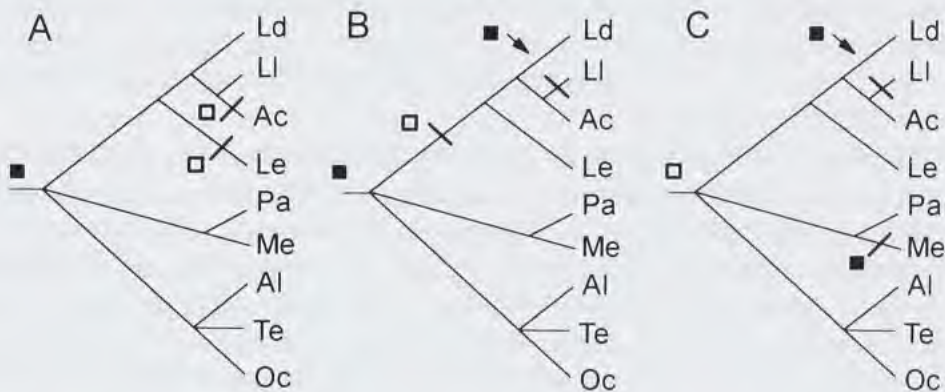


FIG. 21. — Equally parsimonious scenarios for the evolution of the courting song in the *Luzarida* group. Symbols: black square: presence; empty square: absence; thick line: evolutionary change. Names of taxa as in figure 20.

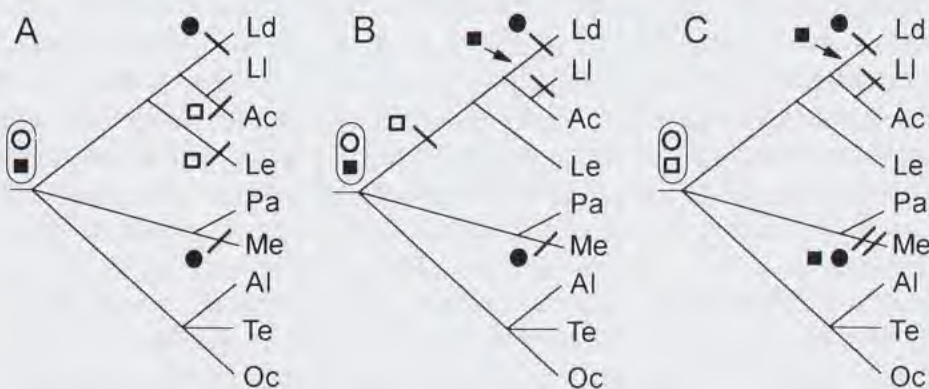


FIG. 22. — Equally parsimonious scenarios for the evolution of the singing ability in the *Luzarida* group. Symbols as in figures 20-21; ancestral states of attributes indicated in a frame. Names of taxa as in figure 20.

ancestrally deprived of a calling song. If the combination (Call. Court. Aggr.) was to occur in these clades, owing to additional data for presently unstudied taxa, it would consequently constitute a derived condition. Moreover, the combination (Call. Court. -), which characterizes *Amphiacusta*, is not predicted by the model. Again the current model on the acoustic evolution of crickets is only partly supported and is unable to explain the observed situation. Similarly, none of the phylogenetic patterns presented here is congruent with the theoretical patterns of figure 9, which means that the hypothesis of a linear loss of the songs is not supported by either the *Amphiacustae* or the *Luzarida* group case studies.

The fact that current hypotheses on the acoustic evolution of crickets are not supported by the phylogenetic analyses of the presence/absence of the songs, means that this evolution cannot be summarized as mere multiple, progressive losses of songs. The phylogenetic analyses show that neither the song combinations nor the polarization of character changes are only those predicted by the model: other possibilities are documented, while some of those predicted by the model are not supported. Phylogenetic patterns also suggest additional aspects of song evolution in crickets that have never been expected before. First, reversals may occur. For example a song which was ancestrally lacking in a cricket clade could reappear in a subclade. Such is the case for the calling song in *Luzarida* and *Melanotes* in the *Luzarida* group. Also convergent changes are common in cricket clades, and there is no obligatory series between the possible song combinations. Similar conclusions were drawn from phylogenetic analyses of stridulum evolution (DESUTTER-GRANDCOLAS, 1996).

The complexity of the phylogenetic patterns that described the evolution of song and stridulum in the studied cricket clades is not a unique phenomenon. Many authors have re-examined evolutionary hypotheses in a phylogenetic framework and documented complex phylogenetic patterns, among which reversals are far from being unusual (ANDERSEN, 1979, 1994; CODDINGTON, 1988; CARPENTER, 1989; WANNTORP *et al.*, 1990; BROOKS & MCLENNAN, 1991; PACKER, 1991; SIDDALL *et al.*, 1993; DESUTTER-GRANDCOLAS, 1993a, 1994a; ANDERSEN & WEIR, 1994; GRANDCOLAS, 1996; many contributors, this volume). One consequence of these results however is that the evolution of acoustic communication in crickets may have been much more complicated than previously thought, at least in some cricket clades. The previous model constructed to explain the evolution of acoustic communication in crickets *s.l.* hypothesized quite simple transformation series. These series were in turn documented in relatively homogeneous groups (mostly gryllid taxa), which populations could be easily studied. When a wide diversity of tegminal structures and communication signals is involved, as in Phalangopsidae for example (Figs 2-8), this model becomes inefficient. GRANDCOLAS *et al.* (1997, this volume) denounced the sampling bias that can be generated in phylogenetic reconstructions by the properties of the clades under study: a clade that presents a wide diversity of features has experienced a larger number of evolutionary events than a clade which is relatively homogeneous for the same features. The study of a diverse clade may consequently lead to overestimate the frequency of evolutionary changes and events. On the reverse, studies of poorly diverse clades may conclude to low frequencies of evolutionary transformations. These biases do not invalidate the results obtain in each case. On the contrary a general theory on the acoustic evolution of crickets will have to explain the complicated cases documented in the Phalangopsidae, as well as the more simple ones that could be found in other cricket groups.

Which factors may have influenced the acoustic evolution of crickets?

Answers to this question have always been based on the assumption that acoustic signals only evolve by song and stridulum loss in crickets (ALEXANDER, 1962, 1967; OTTE, 1977, 1992; WALKER & MASAKI, 1989; BAILEY, 1991). A similar approach was adopted by studies of population biology dealing with song abilities and mating success (THORNHILL & ALCOCK, 1983; HUBER *et al.*, 1989; BAILEY, 1991). The phylogenetic analyses presented here clearly demonstrate that such is not the case: on the contrary, the acoustic evolution of crickets involves a high level of homoplasy. The hypotheses formulated up to now to explain the acoustic evolution of crickets have thus always been biased from the start, because an unwarranted hypothesis (a supposed evolutionary tendency to acoustic loss) was considered attested. As such, these hypotheses are unable to test whether loss actually occurred, or whether other evolutionary changes may have existed. One consequence is that no sound hypothesis exists now on the factors that could have influenced the acoustic evolution of crickets. Another problem, as already mentioned previously, is that the hypotheses that have been proposed up to now are not mutually exclusive. Thus the combination (- Court. Aggr.) could be used as evidence for the influence of predation, inefficiency of acoustic communication, population structure and habitat. Ultimately this means that the hypotheses that have been proposed up to now on the subject could be conclusively tested in a population perspective but not in a historical perspective, although they are supposed to concern evolutionary processes *sensu lato*.

What arguments have been used to support these hypotheses of acoustic evolution of crickets? And have they already been analyzed in a phylogenetic framework? Although cricket predation *s.str.* by many vertebrates and invertebrates has been recorded (WALKER & MASAKI, 1989), its actual pressure has never been measured. Predation by bats in particular has been assumed to be heavy. Some cricket species do show a high acoustic sensibility to ultrasound stimuli, which has been demonstrated to induce negative phonotaxis in flight patterns (SALES & PYE, 1974; HUBER *et al.*, 1989; HOY, 1991). Many mute taxa live however in habitats that are not accessible to bats, such as leaf litter, tree hollows, burrows, etc., and still more acoustic or non-acoustic species do not fly. The effect of parasites on the other hand, especially that of tachinid flies, has been documented in populations of a few cricket species. In these infested populations, some silent males, called satellites, stay near calling males and try to intercept the females attracted by the songs of the calling males (CADE, 1975). It has been suggested that this behavior could be an adaptation to avoid parasitoid infestation and constitute an alternative strategy for mating (THORNHILL & ALCOCK, 1983; BAILEY, 1991). ADAMO *et al.* (1995) show however in *Gryllus integer*, *G. bimaculatus* and *G. rubens* that infestation enhances the tendency of male crickets to mate, at least until tissue damage by the parasite is too high. Also ZUK *et al.* (1995) demonstrate that in a polymorphic population of *Teleogryllus oceanicus* silent males were either parasitized, or able to switch to calling behavior depending on population density. The effect of parasites on calling behavior is thus manifold in cricket populations and depends on the conditions in which the populations live. Its effect on the evolutionary change of acoustic behavior is then hard to predict for the moment until changes may have been actually fixed in taxa (SCHULTZ *et al.*, 1996). A phylogenetic test of predation pressure could be achieved by optimizing escape and acoustic behaviors displayed by the taxa; additional field work is then necessary to characterize such behaviors.

The role of the habitat in the acoustic evolution of crickets has been tested using phylogeny in the Amphiacustae (DESUTTER-GRANDCOLAS, 1995b). In this study, the phylogenetic patterns suggested that the habitat alone cannot have been a sufficient factor to drive the acoustic evolution of crickets. For example taxa living in caves either are wingless, or have a complete, functional stridulum. Similarly in one given habitat, several acoustic behaviors can be found (DESUTTER-GRANDCOLAS, *op. cit.*). Population structure could be a more promising factor in this matter, but unfortunately field data are extremely sparse. Only one taxon, *Nemoricantor maya* (Amphiacustae), has been studied in natural and laboratory conditions: it is gregarious, living in hollow trees, and has no calling song (BOAKE, 1984a, 1984b). Lack of comparative data impedes attempts to determine the role of habitat and population structure on song evolution. Here again combined analysis of phylogeny on one hand, and habitat and population structure on the other should permit a test of the gregariousness hypothesis.

Finally, male crickets may have glands in many parts of their body. Metanotal glands are better known, but others exist on the hindtibiae, the wings, the tergites, the base of some sclerites in male genitalia, etc. (OTTE, 1992; DESUTTER-GRANDCOLAS, 1995b). The only phylogenetic analyses to date of glandular evolution in male crickets (Amphiacustae: DESUTTER-GRANDCOLAS, 1995b) uncovered no shift from acoustic to chemical communication systems, except for the absence of metanotal gland in wingless taxa (probably for lack of protective structure for the glands).

Up to now, most studies on the acoustic evolution of crickets have combined assumptions on the patterns and assumptions on the processes, deriving the one from the other. Phylogenetic analyses confront a phylogenetic pattern, built with as few hypotheses as possible, with independently constructed hypotheses on the evolutionary processes (GRANDCOLAS *et al.*, 1994). They actually test the hypothesized processes with the phylogenetic patterns, the independence of the two sets of assumptions giving this method its power (GRANDCOLAS *et al.*, 1997, this volume). Phylogenetic analyses have been applied here for the first time to the acoustic evolution of crickets. These analyses have demonstrated that current hypotheses on the matter are largely insufficient and biased. Instead they suggest far less simple scenarios for this evolution with high homoplasy. They also clearly demonstrate that no sound hypothesis exists now on the factors that could have influenced cricket acoustic evolution. In fact more phylogenies and more population studies are needed to build new hypotheses.

ACKNOWLEDGEMENTS

The subject of this paper has been presented during the symposium "Phylogenetic tests of evolutionary scenarios" organized by P. GRANDCOLAS (E.P. 90 CNRS, Muséum National d'Histoire naturelle, Paris) in Paris (3-4 June 1996), with the financial support of the Réseau National de Biosystématique (ACC-SV7). I thank three referees for their very useful comments on the manuscript, and J. BOUDINOT, M. FRANEY, G. HODEBERT for their help concerning the figures.

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